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# A multivariate morphometric study of *Senecio paludosus* L. (Asteraceae) in Central and Western Europe

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## Abstract

Hodálová I., Grulich V. and Marhold K. 2002. A multivariate morphometric study of *Senecio paludosus* L. (Asteraceae) in Central and Western Europe. Bot. Helv. 112/2: 137–151.

A multivariate morphometric study of *Senecio paludosus* L. from Central and Western Europe, with additional material from other neighbouring areas is presented. Three subspecies, namely *S. paludosus* L. subsp. *paludosus*, *S. paludosus* subsp. *angustifolius* Holub and *S. paludosus* subsp. *lanatus* Holub are recognised. Principal coordinate analysis confirmed good morphological separation of the above-mentioned taxa using quantitative and qualitative characters with only a few intermediates. The recognition of *S. paludosus* subsp. *bohemicus* (Tausch) Čelak. as a separate subspecies was not confirmed.

**Key words:** *Senecio paludosus*, Asteraceae, Europe, taxonomy, distribution.

## Introduction

The distribution area of *Senecio paludosus* L. ranges from Western Europe to Western Asia. Some European Floras report this species as present also in North America (Nyárády 1964), but there are no concrete data for this area and neither Kartesz (1994) nor Kartesz and Meacham (1999) include this taxon in their works. It is a highly vari-

able species comprising several taxa whose separation and distribution areas are still unclear. Holub (1962) attempted to segregate *S. paludosus* into four subspecies: subsp. *tomentosus* Čelak., subsp. *angustifolius* Holub, subsp. *lanatus* Holub and subsp. *bohemicus* (Tausch) Čelak. The Holub's concept, however, was not accepted by Chater and Walters in *Flora Europaea* (1976) with the following comment: "Subspecies have been described, but are too poorly differentiated both morphologically and geographically to be worth maintaining". *Senecio paludosus* was presented here as a single species without any infraspecific taxa. This view was followed by authors of most local Floras and Checklists (Pignatti 1982, Wagenitz 1987, Kerguélen 1993, Adler et al. 1994, Rothmaler 1994, Wisskirchen and Haeupler 1998, Tasenkevich 1998, Mosyakin and Fedorovichuk 1999). Hess et al. (1972) noted that most of the material from the area of Switzerland corresponded either to subsp. *angustifolius* or possessed characters of both subsp. *angustifolius* and subsp. *tomentosus*. As a consequence they hesitated to recognise subspecies of *S. paludosus* for the area of Switzerland. Soó (1970) and Horváth et al. (1995) recognised subsp. *paludosus* and subsp. *lanatus* for the area of Hungary, and Kucowa (1971) apart from typical populations of *S. paludosus* reported var. *tomentosus* (Host) W. D. J. Koch in Poland. Nyárády (1964) reported three varieties for Romania: var. *glabratus* W. D. J. Koch, var. *tomentosus* (Host) W. D. J. Koch, and var. *procopianus* Hormuz. Among the morphological characters used for the distinction of the infraspecific taxa of *S. paludosus*, the following have been given by the above-mentioned authors: indument of achenes and leaves, leaf margin, shape of leaves and leaf base (Kucowa 1971, Nyárády 1964, Holub 1962). Taxonomic evaluation of infraspecific taxa of *S. paludosus* is complicated by rather confusing pattern of morphological variation (including morphologically intermediate types) and partial sympatry of previously recognised taxa. These facts prompted us to study populations of *S. paludosus* in detail.

Multivariate morphometric approach was applied in the present study to characterise the pattern of variation in qualitative and quantitative morphological characters of *S. paludosus* in the area of Central and Western Europe, and to revise taxonomic concept proposed by Holub (1962).

As a result of our study we propose to recognise three subspecies in Central and Western Europe and neighbouring areas: *Senecio paludosus* L. subsp. *paludosus* (incl. subsp. *tomentosus* Čelak. and subsp. *bohemicus* (Tausch) Čelak.), *S. paludosus* subsp. *angustifolius* Holub and *S. paludosus* subsp. *lanatus* Holub.

## Material and Methods

For morphometric evaluation, herbarium specimens from the following herbaria were used: BM, BP, BRA, BRNM, BRNU, M, MMI, P, PR, PRC, ROZ, SAV, SLO, W, WU, Z. In order to ascertain taxonomical value of the plants corresponding to the name *S. paludosus* subsp. *bohemicus*, two population samples of altogether 200 plants that showed morphological characters of both typical subsp. *paludosus* and subsp. *bohemicus* were also studied. The morphological analyses included in total 768 individuals covering the area of Central and Western Europe and neighbouring areas: Great Britain, France, the Netherlands, Belgium, Switzerland, Germany, Austria, Italy, Slovenia, Hungary, Czech Republic, Slovakia, Poland, Ukraine, Romania, Croatia, Serbia and Montenegro; a few specimens from Sweden, Bulgaria, Lithuania, Latvia, Byelorussia and W Russia were also included (see Appendix). Most of the area of Rus-

sia, however, was not included in this study. The nomenclatural types (or other original material) of *Senecio bohemicus* Tausch, *S. paludosus* subsp. *angustifolius* Holub, *Senecio paludosus* subsp. *lanatus* Holub and *Senecio paludosus* subsp. *tomentosus* Čelak. were included as well.

For the multivariate morphometric study four quantitative and two qualitative characters were measured or scored for each plant. These included characters traditionally used for the identification of the taxa within *S. paludosus* and also those considered as useful by Holub (1962). Quantitative characters: length of stem leaves (LL), width of stem leaves (WL), width of base of stem leaves (WBL) and ratio LL/WL; leaves were measured in the middle part of the stem. Qualitative characters: indument of achenes, coded as a three-state character [1 – glabrous (IAG), 2 – hairy on whole surface (IAS), 3 – hairy in the upper part only, otherwise glabrous (IAU)]; indument of lower surface of leaves as a five-state character [1 – glabrous (ILG), 2 – hairy (with short articulate hairs; ILH), 3 – arachnoid (ILA), 4 – lanate (ILL), 5 – mixed type of indument: arachnoid with short articulate hairs on the same plants (ILM)]. In defining “lanate” and “arachnoid” surface of leaves we follow Jackson (1953) and Stearn (1995). In the arachnoid type epidermis is clearly visible through the meshes of the web formed by hairs, while in the case of the lanate type, the surface of leaves is completely covered by hairs.

The morphometric analyses were performed using the individual specimens as OUTs as follows:

- (1) Principal coordinate analyses (PCoA), using the Gower's coefficient (Podani 2001) were performed on two different data sets: (a) a set of the herbarium specimens and two mixed population samples of *S. paludosus* subsp. *paludosus* and plants corresponding to *S. paludosus* subsp. *bohemicus*, (b) a set of the two above-mentioned mixed population samples. This method was used in order to generate a hypothesis suggesting a possible grouping of the individuals studied.
- (2) Correlation between the principal coordinate axes and original quantitative characters was computed using Pearson's correlation coefficient.
- (3) Basic statistics of quantitative characters (mean, minimum and maximum values, coefficient of variation, and standard deviation) for each group resulting from PCoA as well as frequencies of character states of qualitative characters were computed.

In the interpretation of the ordination diagrams, the group assignation of the particular specimens was based on their morphological characters and geographic occurrence. Apart from the groupings that were possible to ascribe to already recognised subspecies and which occupy some definable area, there were few ones, which represented plants that we call “intermediate”. These plants usually possessed characters of more than one subspecies grouping and came from scattered localities from the whole area studied. In some cases “intermediate” individuals were found also within the main subspecies groupings. All such intermediate plants are marked in the ordination diagrams and discussed separately.

All analyses were carried out using the SAS statistical package at the Charles University, Prague (SAS Institute 2000) and the program SYN-TAX 2000 for Windows (Podani 2001).

Scanning electron microscopic (SEM) studies were carried out at the Dionýz Štúr State Geological Institute, Bratislava.

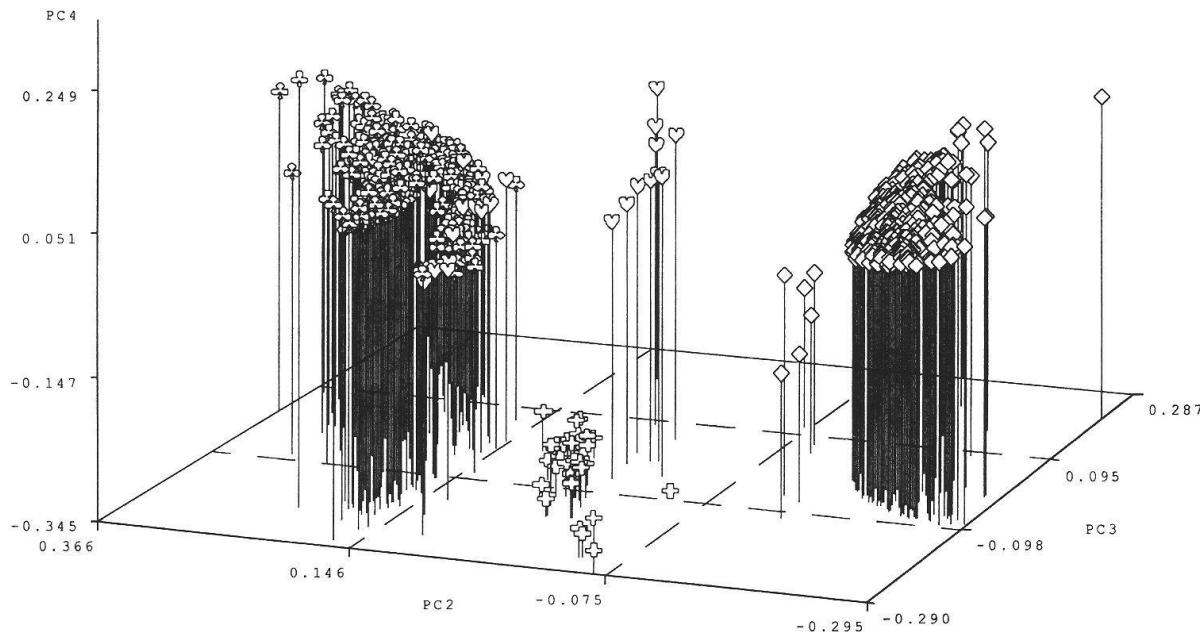


Fig. 1. Ordination diagram of the principal coordinate analysis of *Senecio paludosus* subsp. *paludosus* (club), *S. paludosus* subsp. *angustifolius* (diamond), *S. paludosus* subsp. *lanatus* (cross), intermediate specimens between *S. paludosus* subsp. *paludosus* and *S. paludosus* subsp. *angustifolius* (heart). The first three axes account for 55.44, 11.94 and 7.35% of variation, respectively.

## Results

### Principal coordinate analyses

Two principal coordinate analyses were performed. The PCoA, based on the complete data set (PCoA(a), Fig. 1) depicts four more-less distinct groupings. The grouping of *S. paludosus* subsp. *paludosus* (marked as clubs, 310 plants) is on the left side, that of subsp. *angustifolius* (marked as diamonds, 397 plants) on the right side of the diagram. The grouping of the latter subspecies includes also six plants in a somewhat remote position, but they still could be safely classified as subsp. *angustifolius*. Only one plant of them [originating from Kecskemét, river Tisza [Tibiscum], meadow Sziksa (Dorner 1866 BP)] possessed leaf indument which was more close to subsp. *lanatus*. Between these two main groupings, there is a group of subsp. *lanatus* (marked as crosses, 33 plants), and a group of plants intermediate between subsp. *paludosus* and subsp. *angustifolius* (marked as hearts, 10 plants). The latter group consists of plants of various geographical origin (e.g. the Netherlands, France, Germany). These plants possess hairy achenes (typical for subsp. *paludosus*) and arachnoid indument of lower surface of leaves (typical for subsp. *angustifolius*). In addition to them, there are 18 intermediate plants (marked also as hearts) included in the grouping of subsp. *paludosus* on the left side of the ordination graph. Although they are not grouped together with other plants intermediate between subsp. *paludosus* and subsp. *angustifolius*, they showed similar morphology to them. As in the case of the above-mentioned 10 intermediate plants, these plants possess hairy achenes, however, the indument of lower surface of leaves is

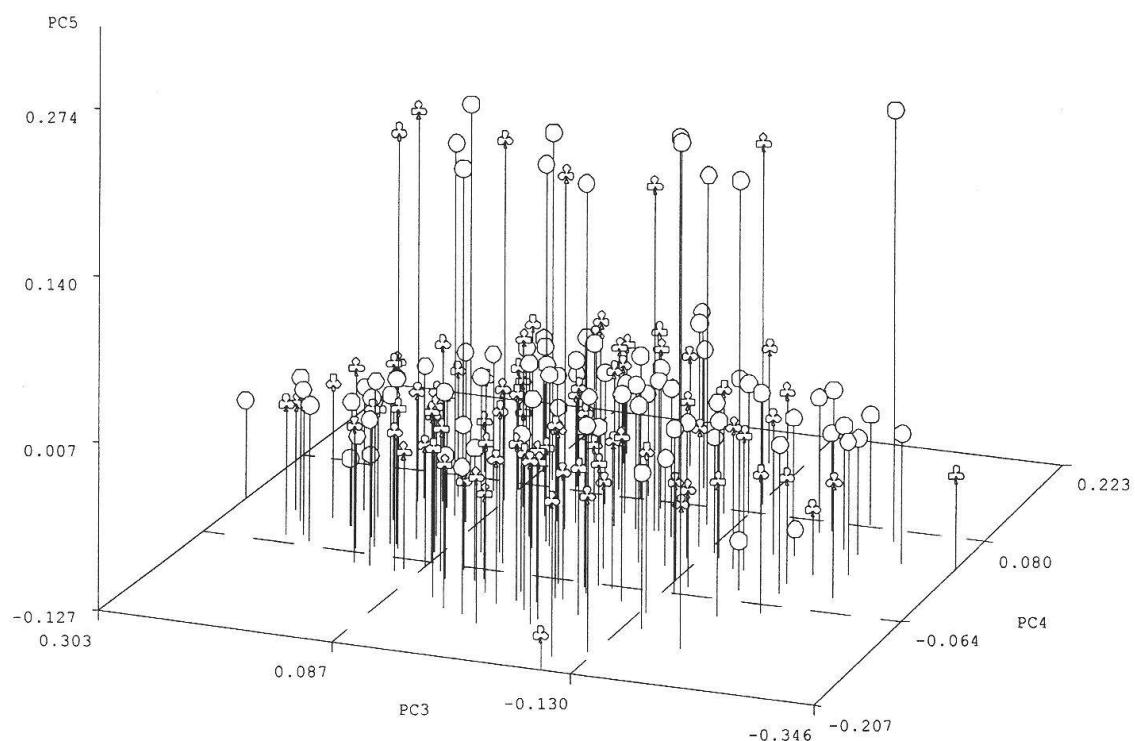


Fig. 2. Ordination diagram of the principal coordinate analysis of two population samples of *Senecio paludosus* subsp. *paludosus* corresponding to typical subsp. *paludosus* (club) and plants sometimes called as subsp. *bohemicus* (Holub 1962) (ball). The plants were assigned to two groups and correspondingly marked according to their indument. The first three axes account for 42.67, 21.66 and 10.39% of variation, respectively.

of mixed type (ILM). The following quantitative characters were most correlated with the first and second axes (value of correlation coefficient in brackets): with PCo1 characters WL (0.75658) and LL/WL (-0.61669); with PCo2 characters LL (0.67666) and WBL (-0.73380). No character was particularly correlated with the third axis.

In the description of *S. bohemicus* Tausch (Syll. Ratisb. 2: 253, 1928) stressed, among other characters, the following "...foliis lanceolatis serratis, basi attenuates subpetiolatis glabris ac vix floccosis". According to Holub (1962) *S. paludosus* subsp. *bohemicus* and *S. paludosus* subsp. *paludosus* (= *S. paludosus* subsp. *tomentosus* (Tausch) Čelak.) differ only by indument of lower surface of leaves. The former possess hairy leaves (with short articulate hairs) while the latter has leaves glabrous beneath. The original material of the name *S. bohemicus* Tausch (Holub 1962, Marhold, Grulich and Hodálová, in prep.) has leaves glabrous beneath. Detailed study of two population samples of *S. paludosus* corresponding to typical subsp. *paludosus* and plants called as subsp. *bohemicus* (PCoA(b), Fig. 2) showed that both morphological types occur within the same population and there is no correlation of variation of indument of lower surface of leaves with other morphological characters. The principal coordinate analysis of both population samples (200 plants altogether) performed without taking into account indument of leaves did not show any groupings whatsoever.

Tab. 1. Variation in the character indument of achenes in *Senecio paludosus* subsp. *paludosus* (PAL; n = 310), *S. paludosus* subsp. *angustifolius* (ANG; n = 397), *S. paludosus* subsp. *lanatus* (LAN; n = 33), intermediate specimens between *S. paludosus* subsp. *paludosus* and *S. paludosus* subsp. *angustifolius* (PAL/ANG; n = 28), expressed as the frequency of character states. (IAG – glabrous, IAS – hairy on whole surface, IAU – hairy in the upper part only).

Character/Taxon	IAG	IAS	IAU
PAL	0	310	0
ANG	377	20	0
LAN	0	2	31
PAL/ANG	0	28	0

Tab. 2. Variation in the character indument of lower surface of leaves in *Senecio paludosus* subsp. *paludosus* (PAL; n = 310), *S. paludosus* subsp. *angustifolius* (ANG; n = 397), *S. paludosus* subsp. *lanatus* (LAN; n = 33), intermediate specimens between *S. paludosus* subsp. *paludosus* and *S. paludosus* subsp. *angustifolius* (PAL/ANG; n = 28), expressed as the frequency of character states.

(ILG – glabrous, ILH – hairy (by short articulate hairs), ILA – arachnoid, ILL – lanate, ILM – mixed type of indument: arachnoid with short articulate hairs on the same plants).

Character/Taxon	ILG	ILA	ILH	ILL	ILM
PAL	103	0	204	0	3
ANG	1	396	0	0	0
LAN	0	0	0	33	0
PAL/ANG	0	10	0	0	18

### Exploratory data analysis

Results of the exploratory data analysis indicate that all three subspecies: *S. paludosus* subsp. *paludosus*, *S. paludosus* subsp. *angustifolius* and *S. paludosus* subsp. *lanatus* can be distinguished predominantly by qualitative characters – indument of achenes and lower surface of leaves (Table 1, 2, Fig. 3). The plants intermediate between subsp. *paludosus* and subsp. *angustifolius* possess indument of achenes typical for subsp. *paludosus*, indument of lower surface of leaves is usually mixed (ILM) or they possess indument typical for subsp. *angustifolius*. The ranges of quantitative characters WL and LL/WL only slightly overlap between subsp. *paludosus* and subsp. *lanatus* on one hand, and subsp. *angustifolius* on another (Table 3). The leaves of subsp. *paludosus* and subsp. *lanatus* are broader (anguste-ovate to ovate) than those of subsp. *angustifolius* that are lanceolate. Certain differences can be seen also in characters LL and WBL, however, there is a lack of clear morphological discontinuities in these characters.

### Discussion

Our results showed that morphological variability within *S. paludosus* is not random, but it is possible to recognise three subspecies in the area studied. The combination of several correlated characters, including indument of achenes, and indument and

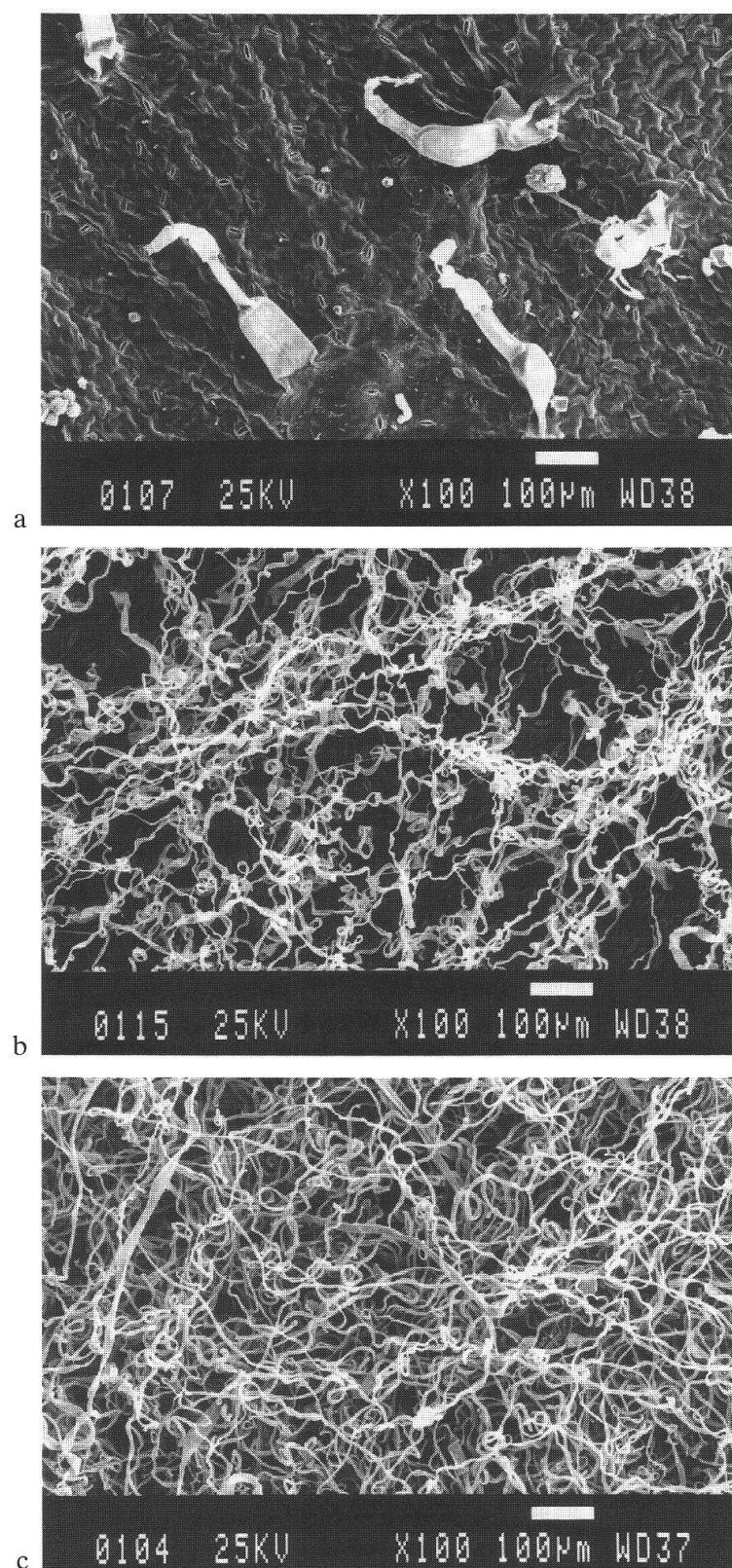


Fig. 3. Scanning electron micrographs of indument of lower surface of leaves: a) in *Senecio paludosus* subsp. *paludosus* short articulate hairs, ILH), b) in *S. paludosus* subsp. *angustifolius* (arachnoid type of indument, ILA), and c) in *S. paludosus* subsp. *lanatus* (lanate type of indument, ILL).

Tab. 3. Summary statistic for quantitative characters of *Senecio paludosus* subsp. *paludosus* (PAL; n = 310), *S. paludosus* subsp. *angustifolius* (ANG; n = 397), *S. paludosus* subsp. *lanatus* (LAN; n = 33), and intermediate specimens between *S. paludosus* subsp. *paludosus* and *S. paludosus* subsp. *angustifolius* (PAL/ANG; n = 28) (% – percentile).

Character	Taxon	Mean/cm	St. deviation	5%	95%
LL	PAL	13.59	± 2.50	8.1	15.85
	ANG	12.22	± 2.54	6.5	13.85
	LAN	11.08	± 2.54	7.1	12.9
	PAL/ANG	13.43	± 3.61	9.3	18.5
WL	PAL	1.96	± 0.69	1.2	2.3
	ANG	1.02	± 0.39	0.7	1.2
	LAN	1.64	± 0.64	1.3	2.0
	PAL/ANG	1.52	± 0.53	0.8	2.6
WBL	PAL	0.61	± 0.26	0.1	0.8
	ANG	0.54	± 0.22	0.1	0.7
	LAN	0.45	± 0.20	0.2	0.5
	PAL/ANG	0.56	± 0.25	0.2	1.0

shape of leaves (see the identification key), can be used for distinguishing them. *S. paludosus* subsp. *paludosus* is characterised mainly by the achenes hairy thorough their entire surface and by leaves glabrous to hairy beneath. On the other hand, *S. paludosus* subsp. *angustifolius* has glabrous achenes and leaves arachnoid beneath. *S. paludosus* subsp. *lanatus* possesses achenes hairy in upper part only and leaves lanate beneath.

The above-mentioned taxa have their own distribution areas (although to some extent overlapping; Fig. 4, 5). *S. paludosus* subsp. *angustifolius* seems to be slightly oceanic and more thermophilous taxon occurring in the western and middle part of Europe. The eastern limit of its distribution crosses Germany, Czech Republic, Southern Slovakia, Hungary and reaches the area of Southern Romania and Serbia and Montenegro.

*Senecio paludosus* subsp. *paludosus* as a more continental and less thermophilous taxon was confirmed in Northern, Central and Eastern Europe. The western distribution limit crosses Sweden, Germany, Austria and Croatia. To the south of the continuous area of this subspecies, there is isolated occurrence in the mountainous areas of Styria and the Balkan Peninsula.

Intermediate plants between *S. paludosus* subsp. *angustifolius* and subsp. *paludosus*, usually co-occurring with the typical subsp. *paludosus* or subsp. *angustifolius*, have been observed in the area where both subspecies grow, namely in Germany, Austria, Czech Republic and Slovakia (Fig. 4) and they might result from recent introgression between these two taxa. However, intermediates can be found also in certain areas where typical representatives of *S. paludosus* subsp. *paludosus* are lacking (see above-mentioned distribution of subsp. *paludosus*), e.g., in the Netherlands and NW France. The presence of these intermediates in this part of Europe is more difficult to explain. Their occurrence might be somehow connected with the distribution of subsp. *paludosus* in Scandinavia (as geographically most closest populations) and introgression might have occurred in past. These plants requiring undoubtedly more detailed field studies usually have sparsely or rarely densely hairy achenes (typ-

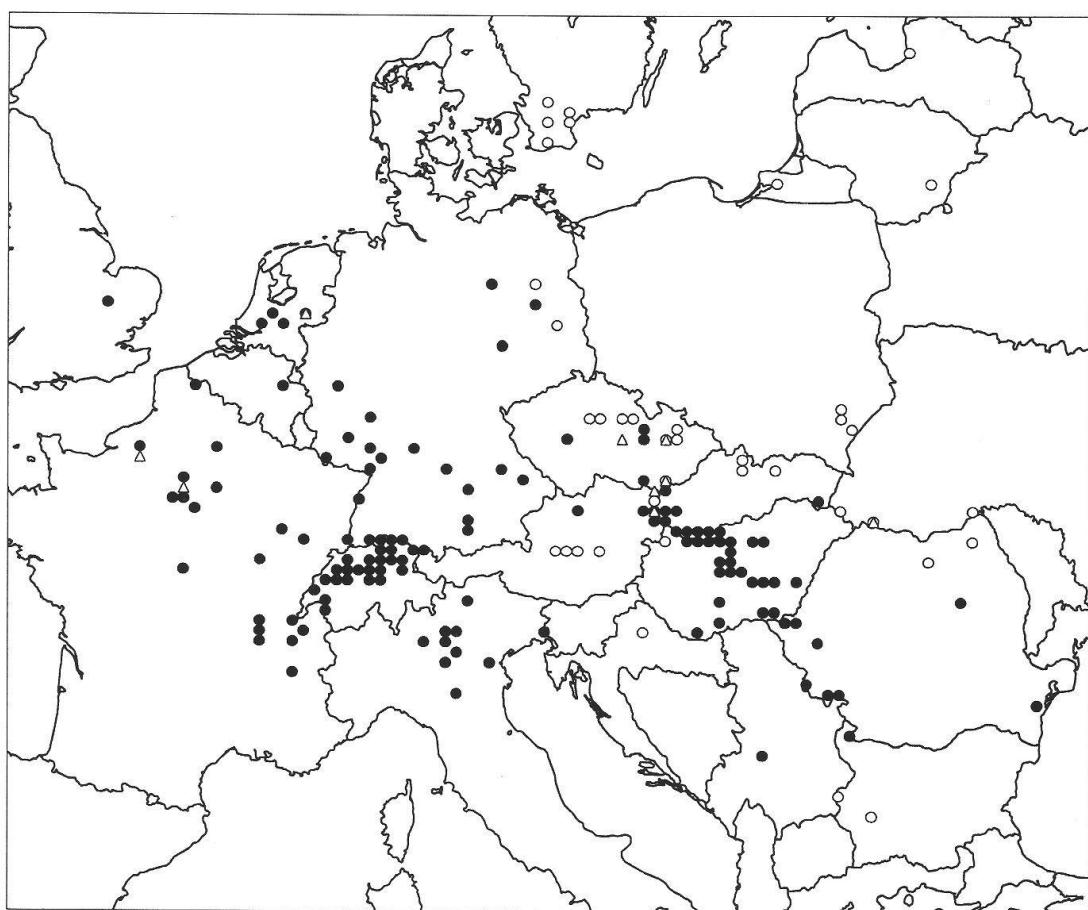


Fig. 4. Distribution map of herbarium specimens used for the morphometric study from Central and Western Europe and neighbouring areas. *Senecio paludosus* subsp. *paludosus* (○); *S. paludosus* subsp. *angustifolius* (●); intermediates between subsp. *paludosus* and subsp. *angustifolius* (△).

ical for subsp. *paludosus*) and arachnoid lower leaf surface (typical for subsp. *angustifolius*), or lower leaf surface indument is of mixed type between subsp. *angustifolius* and subsp. *paludosus*.

*Senecio paludosus* subsp. *lanatus* was confirmed in the Central and Eastern Europe (Hungary, Czech Republic, Slovakia, Ukraine, Romania, Byelorussia, Russia). Although reported by Kucowa (1971) from Poland [as *S. paludosus* var. *tomentosus* (Host) W. D. J. Koch], there was no specimen of subsp. *lanatus* from this area in our studied material, but its occurrence there cannot be excluded.

All three taxa *S. paludosus* subsp. *paludosus*, *S. paludosus* subsp. *angustifolius* and *S. paludosus* subsp. *lanatus* occupy localities with similar ecological conditions and are restricted to wet places with standing or slowly flowing water.

*Senecio paludosus* subsp. *bohemicus* has been sometimes separated from subsp. *paludosus* by having glabrous leaves on lower surface, in contrast to leaves hairy beneath reported for subsp. *paludosus* (Holub 1962). However, in populations of subsp. *paludosus* plants with both glabrous and hairy leaves can be found and in the some case both types were observed on the same plant individual. Thus, due to the absence

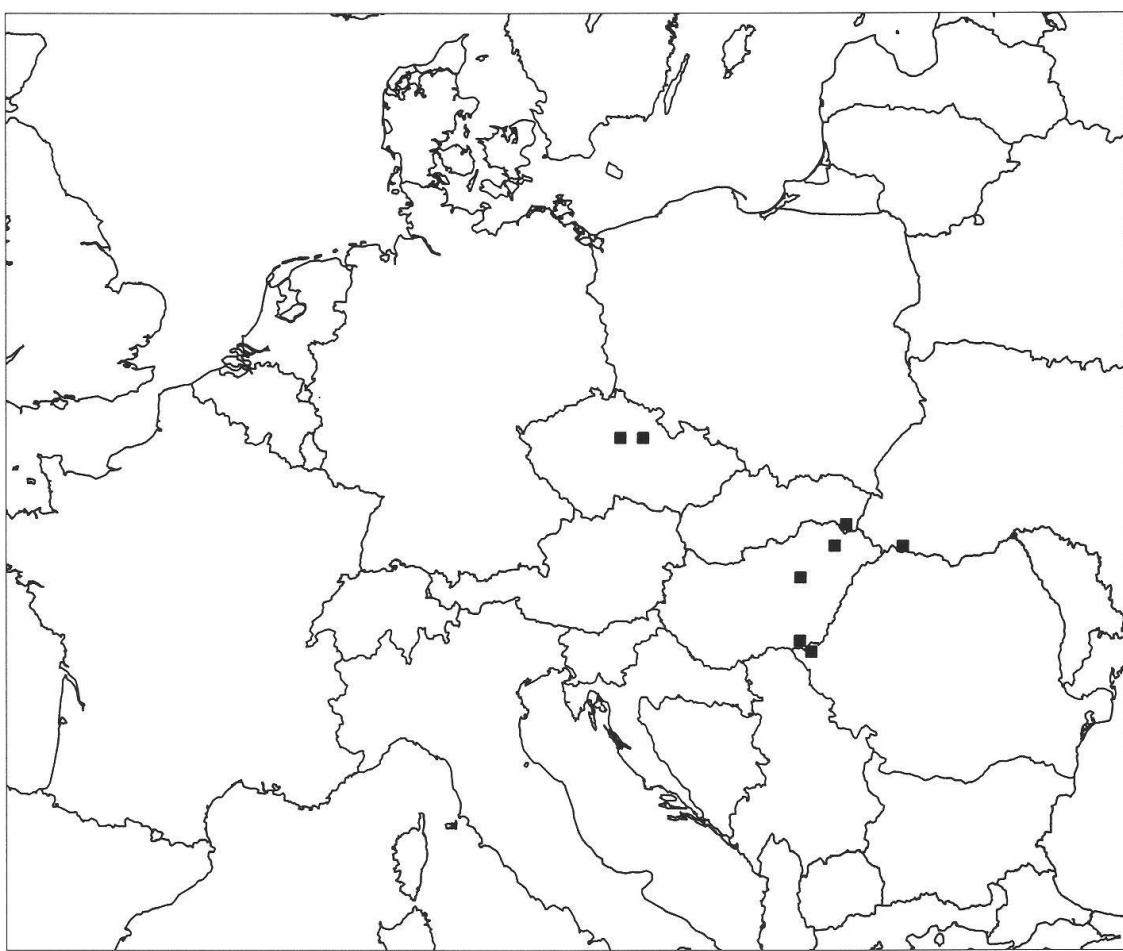


Fig. 5. Distribution map of herbarium specimens of *Senecio paludosus* subsp. *lanatus* used for the morphometric study from Central Europe.

of any other reliable character separating subsp. *bohemicus* and subsp. *paludosus*, the former one is not recognised here.

The above-mentioned subspecies can be identified using the following key:

Cauline leaves anguste-ovate to ovate, 8.1–15.9 × 1.2–2.3 cm, hairy (mainly with short articulate hairs) or rarely glabrous beneath, achenes hairy on whole surface.....

.....**subsp. *paludosus***  
(Syn.: *Senecio paludosus* subsp. *tomentosus* Čelak., *Senecio bohemicus* Tausch, *Senecio paludosus* subsp. *bohemicus* (Tausch) Čelak., *Senecio paludosus* β *glabratus* W. D. J. Koch)

Plants intermediate between subsp. *paludosus* and subsp. *angustifolius* possess an arachnoid (typical for subsp. *angustifolius*) or mixed (arachnoid with short articulate hairs on the same plants) type of indument on lower leaf surface and achenes hairy on whole surface (typical for subsp. *paludosus*).

Cauline leaves linear-lanceolate to lanceolate, 6.5–13.9 × 0.7–1.2 cm, arachnoid beneath, achenes glabrous .....**subsp. *angustifolius***  
(Syn.: *Senecio paludosus* var. *procopiani* Hormuz.)

Cauline leaves anguste-ovate to ovate, 7.1–12.9 × 1.3–2.0 cm, lanate beneath, achenes hairy in upper part only ..... *subsp. lanatus*  
 (Syn.: *Senecio tomentosus* Host, *Senecio paludosus* var. *tomentosus* (Host) W. D. J. Koch, *Senecio tataricus* Less., *Senecio paludosus* γ *hypoleucus* Ledeb.).

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## Appendix – List of the localities of the herbarium specimens used for the morphometric study

(? – unreadable collectors or data of collection; number of specimens studied in brackets, set in italics; <=> – indicates intermediacy between two subspecies)

### *Senecio paludosus* L. subsp. *paludosus*

**Sweden:** Skåne: Sjöholmen (Montelin 1907 PRC). \*Bosarp (Ahnfelt s. d. BM). \*lake Ringsjön [Höör] (Andersson 1884 BRA). \*Kristianstad (Anderson 1846 P; Melandes 1869 BM; Wallengren 1889 BM; 1887 SLO). \*between Kristianstad and Björket (Lange 1922 BM). \*Hammar (? 1891 BM; Björnström 1941 Z). \*Paroecia Gustav Adolf, Håslöv (Hasslov 1931 BM; W). \*Skåne (Andersson s. d. W (2); Ångström 1846 W; Domin 1907 PRC) – unmapped records. **Germany:** Oranienburg (Schultz s. d. Z). \*Lübben (Stendell 1878 Z). **Austria:** Öblarn (Hayek 1901 BRA; WU (2); Witasek 1901 WU). \*Trautenfels am Grimming (Höpflinger 1950 Z; W). \*between Stainach and Irdning (Vetter 1903 W). \*Gaishorn (Schneider s. d. W; Hayek 1899 WU; Fleischmann 1904 W; WU; Z; Zerny 1912 W). \*Einöd (Möschl and Pittoni 1974 BM; Z). \*Stillfried (Polak s. d. PRC). **Hungary:** Mosonszentjános (Kárpáti 1931 BP). **Czech Republic:** Sadská (Hansgirg 1882 PR). \*Poděbrady (Čelakovský 1867 PR). \*Libice nad Cidlinou (Tausch s. d. W (3)). \*Třebechovice p. Orebem (Šourek 1942 BRA; PR). \*Petrovice (Souček s. d. PRC; Souček 1929 BRNM). \*Týniště nad Orlicí (Rohlena 1921 PRC). \*between Týniště and Orlicí and Častolovice (Rohlena 1920 PRC; 1921 PRC). \*Kostice (Staněk 1945 BRNM). \*Tvrdonice (Staněk 1945 BRNM). \*Střeň (Otruba 1927 BRNM). \*Hlušovice (Čoka 1906 BRNU; PRC). \*Olomouc (s. d. s. coll. BRNM; s. coll. s. d. W; Hayne s. d. W; Otruba 1942 PRC). \*Moravský Písek (Bílý 1923 BRNM). \*Krahulčí (Štěpánek 1989 PR; Grulich 2000 BRNU (100)). \*Roudno (Ringer 1893 BRNU; PRC; 1907 BRNM; Grulich 2000 BRNU (100)). **Slovakia:** Lúčky (Hazslinszky s. d. BP; BRA; SLO; s. coll. 1808 W; Rochel 1808 PR; Bohatsch 1874 BP; Wetschky 1889 BP; s. coll. 1937 SAV; Nábělek 1937 SAV; 1940 SLO; Staněk 1947 BRNM (2); Dvořák 1955 BRNM). \*between Ústie nad Priehradou [Hamry] and Bobrov (Holub 1951 PRC (2)). \*Liptovská Teplá (Jermy s. d. Z) – unmapped record. **Poland:** Nowy Dwór Gdańsk [Tiegenhof] (Gross 1905 Z). \*Sieniawa (Błocki and Wołoszczuk 1887 W). \*between Starzawa and Nakło (Kotula 1877 W (2)). **Ukraine:** Buštyna (Vágner s. d. BP (4)). \*Makorovo, Mt. Fornos (Margittai 1917 PRC; PR; Margittai s. d. Scheffer herb. in SLO). \*Colencăuți, river Rachitna (Țopa 1934 W). **Romania:** Cămpulung, Poiana Stampei (Grințescu 1936 W, Z). \*Lueta (Barth 1869 BP). \*Botoșani, Bucecea, river Sirețul (Grințescu 1925 BM; P; PRC; W; Z). **Bulgaria:** Samokov (Velenovský 1889 PRC). **Croatia:** Vrbovec (Berek) (Pevalek 1917 WU). **Federal Republic of Yugoslavia:** lake Vlasinsko Jezero (s. coll. s. d. Z; Ilić s. d. WU; Adamović 1897 W). **Lithuania:** Vilnius, river Viliia (Symonowicz 1899 PRC). **Latvia:** Saulkrasti (Zinger and Finn 1903 BM; M; W). **Russia:** Kaliningrad (Rabnitz 1868 BM; Ginzberger 1920 WU). \*Flora Ingricae, river Neva (s. coll. 1860 W; Meinshausen 1860 BM) – unmapped records.

### *Senecio paludosus* subsp. *angustifolius* Holub

**Great Britain:** Ely (Hanbury 1831 BM). \*Wicken Fen (Bickham 1913; 1915 BM). **France:** Rouen (Schoenefeld 1890 BM). \*Itteville (Delacour 1866 P). \*St. Ouen (Ledien 1884 P). \*Bourges (Chabert 1906 BM; Loret s. d. P). \*Mennecy (Cosson 1841 P). \*Neuilly (Cosson 1839 P). \*Gournay sur Marne (Camus 1898 P). \*Chelles (Aimée 1897 P). \*Nemours (Legros 1891 P). \*marais Fourbeux (Emmerin-Nord) (Lamarliére 1888 P). \*Esternay (Gaume 1921 P). \*Urcel, river Aisne, “marais tourbeaux et souvent inondés” (Martin 1889–90 P; W; WU). \*Urcel, river Aisne, “près d’Ardon” (Magnier and Martin 1889 W; WU). \*Anse (Gandoger 1874 PRC). \*Le Chesne (Duvigneaud 1979 M). \*Mâcon (Lacroix 1877 Z (2); Engelhardt 1880 BM (2)). \*Gevrey-Chambertin (Chamberet and Gérard 1914 P). \*Bourg (Géneau de Lamarliére et al. 1889 P). \*Belley (? 1868 Z; Cholin 1919 P). \*Grenoble (Chabert 1845 Z). \*Aix-les-Bains (Bonjean s. d. W). \*Collonges (Sargnon 1884 P). \*Port-sur Saône (Madiot 1932 BM; Z). \*Annecy (Puget 1867 P). \*Neuweg (Elsass) [Bartenheim-la Chaussée] (Fries 1865 Z). \*Neudorf, Ober-Elsass [Neuf] (Rübel 1890 Z). \*Strasbourg (s. coll. 1884 Z; Beik 1884 BM; Garnier 1921 P; Billot fil. 1948 W). Eclaron (Retz 1991 M). **Netherlands:** Jaarsveld (Stafleu 1957 BRNU). \*Tull (Florschütz and

Stafleu 1951 Z). \*Grebbenberg near Rhenen (Ketellapper 1950 BM). \*between Rhenen and Wageningen (Kramer and Mennega 1952 W). \*Wageningen (Middelberg 1911 Z). \*Voorst-Zutphen (Lindeman 1957 Z (2)). **Belgium:** between Hermalle and Herstal (Marchal 1868 BM; PRC). \*between Lierre and ?Embleden (Dewalque 1883 M). \*Belgium (Lejeune and Courtois s. d. BM) – unmapped record. **Switzerland:** river Orbe (Vetter 1882 Z). \*Yverdon (Wolf s. d. Z; Leresche 1843 W). \*Yvonand (Leutwein-de Fellenberg 1852 Z). \*Rivaz (Graber 1919 Z). \*Colombier (Tripet 1872 Z; Wirth 1910 Z). \*Auvernier (Knetsch 1908 Z). \*Vouvry (s. coll. 1875 Z). \*between Vouvry and Roche (Tessier s. d. Z). \*between Vionnaz and Vouvry (Maillefer 1903 PRC; W). \*Villeneuve (? 1902 Z). \*Illarsaz (Farquet 1913 Z). \*Monthei (? 1889 Z). \*Aigle (Favrat 1871 Z; ? 1879. Z (2); Jaccard 1909 Z). \*Chabrey, lake Neuchâtel (Burdet, Charpin, Greuter and Thiébaud 1971 BM; BRA; M; W). \*Le Landeron (Steinmegger s. d. Z; Jeanjaquet 1842 Z). \*Erlach, Peterinsel (Stauffer 1953 Z). \*Erlach (Lüdi 1913 Z; Beger 1942 Z). \*Sugiez (Berger 1943 Z). \*Orpund (Berger 1941 Z). \*Luzern (Ward 1865 BM; Frölich 1904 Z). \*Seedorf (Castella 1909 Z; Jaquet 1916 Z). \*Zollikofen (s. coll. s. d. Z). \*Selzach (Brosi 1953 Z). \*Staad (Schlatter s. d. Z). \*Solothurn (s. coll. s. d. Z). \*Weier (Hägi 1925 Z). \*Menznau (Hugentobler 1942 Z). \*Sempachersee (Schwere 1929 Z). \*Boniswil (Fischer-Sigwart 1890 Z (2)). \*Seengen (Harri 1919 Z; Stauffer 1953 Z; Flück 1946 Z). \*Sulz (Thurnheer 1919 Z). \*Hallwiler See (s. coll. 1890 Z). \*Sachsels (Barlocher 1910 Z; Scherer 1912 Z (2)). \*Koblenz (Koch 1954 Z). \*Hitzkirch (Meier 1906 Z). \*Fischbach (Thellung 1919 Z). \*Rothsee (Neumann 1885 Z). \*Maschwanden (Hegetschweiler 1880 Z). \*Mühlau (Stauffer 1959 Z). \*Geroldswil (Koch 1934 Z). \*Zürich, Altstetten (Rikli 1895 Z (2)). \*Zürich, Oerlikon (Ruhoff 1886 Z; Hanhart 1895 Z). \*Neerach (s. coll. 1946 Z). \*Kilchberg (Baumann 1888 Z). \*Lauerz (Amand 1915 Z). \*Küschnitt (Bredscker s. d. Z). \*Buriet near Rheineck (Buel 1916 Z). \*Brunnen (Kummer 1946 Z). \*Neuhausen am Rheinfall (Kummer 1920 Z). \*Greifensee (Landolt 1946 Z). \*Ossingen (Hägi 1907 Z). \*Weisslingen (Hägi 1928 Z). \*Hombrechtikon (Baumann 1921 Z). \*Diessendorf (Stadler 1875 Z; Baumann 1907 Z). \*Robenhausen am Pfäffiker See (s. coll. 1913 Z; Baltisberger 1973 Z; 1974 Z; 1978 Z; Hartwig 1983 Z). \*Pfäffikon (Keller ? Z; Hägi 1925 Z (2)). \*Grüningen (Hägi 1929 Z). \*Rapperswil (Ley 1875 BM). \*between Jona and Wurmsbach (Koch 1951 Z). \*Bäretswil (Hägi 1901 Z; 1925 Z). \*Stein am Rhein (Vetter 1876 Z; Buel 1879 Z; Baumann 1912 Z; Jaag 1937 Z). \*Hemishofen (Baumann 1921 Z). \*Bleiken-Wattwil (Hagmann 1906 Z). \*Ermatingen (Baumann 1904 Z (3); Baumann 1905 Z). \*Weesen (Däniker 1917 Z; Müller 1930 Z). \*Kreuzlingen (Loretz 1860 Z). \*St. Gallen (Schlaffer s. d. Z; Brockmann 1900 Z; Gadien 1910 Z). \*Salmsach (? 1908 Z). \*Romanshorn (? 1893 Z). \*Horn (Lutz s. d. Z). \*Altenrhein (Koch 1912 Z; Neumann 1967 W). \*Zürichsee (Schulthess 1918 Z) – unmapped record. \*Zürich (Bernoulli 1835 Z; ? 1876 Z) – unmapped record. \*Bodensee (Meister 1881 Z; Boltshauser 1899 Z) – unmapped records. **Germany:** Broich near Kempen (Höppner 1931 M). \*St. Hubert bei Krefeld (Rehnelt 1967 M). \*Bonn (Jurrigen 1893 Z). \*Dürkheim (Palatinat) (Schultz 1844 W; 1841 P). \*Mainz (Ziz ? W). \*Karlsruhe (s. coll. 1860 Z). \*Frankenthal (Zuccarin s. d. M). \*Schifferstadt (Ruppert 1916 M). \*Speyer (Laforç s. d. P; s. d. M). \*Mannheim (Förster 1887 M). \*Rheinau (Förster 1890 M). \*Allensbach, Untersee (Baumann 1905 Z). \*Konstanz (Baumann 1904 Z; Müller 1906 Z). \*Lindau a/ Bodensee (Nábělek 1939 SAV). \*Burlafingen (Renner 1900 M). \*Nordlingen (? s. d. M). \*Wassertrüdingen (Hauser 1848 BM; M). \*Hoppingen (Cramer 1952 M). \*Leitheim (Zinsmeister 1903 M). \*Bertoldsheim (Moulin s. d. Z). \*Amper, near lake Ammersee (Roepler 1957 BM). \*Inninger Baches (Gröger 1986 M). \*Fischen am Ammersee (Hegi 1912 Z). \*Grafrath (Holler 1856 M; Roessler 1957 M). \*Überlinger See, insel Mainau (Knetsch 1900 Z). \*Herrsching (Hegi 1903 Z; Meyer 1906 Z). \*Starnberg (? 1906 M). \*Dachau (Arnold 1907 M). \*between Palzing and Zolling (Sellmair 1973 M). \*Osterburg (Altmark) (Muster 1912 BRNM). \*Regensburg (s. coll. s. d. W). \*Schkeuditz near Leipzig (Petermann s. d. Z). \*Weichs (Schuhwerk 1990 M). \*Geisling (Schuhwerk 1986 M). \*between Marquartstein and Raiten (Merxmüller and Brixle 1933 M). \*Feldwies (Schauer 1966 M). \*Dingolfing (Gierster 1904 M). \*Gottfrieding (Frieber 1939 M). \*between Gottfrieding and Schwaigen an der Isar (Frieberg 1942 M). \*Traundorf (Henle 1914 M). \*Bogen (Herz 1879 Z; Döbbeler and Wenninger 1977 M). \*Inzell (Gützmann 1967 M). \*between Neuötting and Marktl (Oberwinkler 1963 M). \*Potsdam (Hegi 1901 Z; Galasch 1902 Z). \*Vilshofen (Roessler 1960 M). **Austria:** Bregenz (Fenzl s. d. W; Schneider 1912 W; Polatschek 1971 W; Dörr 1986 W (2)). \*Schwarzach (Schwimmer and Buel 1930 Z). \*Lochau

(Dörr 1988 W).\*Klagenfurt (Leute 1990 WU).\*Arbing (Haselberger 1888 WU).\*Klosterneuburg (Keissler 1930 W).\*Bruck an der Leitha (s. coll. 1835 W; Hofmann 1878 W).\*Baumgarten a. d. March (Juratzka 1857 W; Z; Matz 1858 W; WU; Müllner 1878 W).\*Marchegg (Korb 1916 W (2); Schneider 1920 W).\*between Zwerndorf and Baumgarten a. d. March (Korb 1921 W).\*river Russbach in Marchfeld (Aust 1885 W).\*Schlosshof (Reuss 1872 W; Schneider 1899 W; Rechinger 1924 Scheffer herb. in SLO). **Italy:** between Predore and Sarnico, lake d'Iseo (Ronninger 1911 W).\*Bréscia, lake d'Idro (Porta 1871 BM; P).\*Verona, Valeggio s. M., river Mincio (Rigo 1886 PR).\*between Bardolino and Garda (Rigo 1893 M; PR).\*Modena, S. Anna, river Panaro (Mori 1879 Z; Vaccari 1886 M).\*Modena, Valli di Novi (Mori 1879 BRA).\*Bolzano, river Etsch (Hausman s. d. M; Handel-Mazzetti 1905 WU; Z; Vierkapper 1905 Z; Hausman 1932 M).\*between Monselice and Arqua-Petrarca (Béguinot 1911 BM; WU, Z (2)).\*Monfalcone (s. coll. s. d. W; Schneider 1904 W). **Slovenia:** Doleneje Jezero, Cerkniško jezero (Mayer 1977 M).\*between Doleneje Jezero and Otok, Cerkniško jezero (Mayer 1967 M). **Hungary:** Györ (s. coll. 1937 BP).\*Gordisa (Boros 1922 BP).\*Matty (Simonkovics 1873 BP).\*Esztergom (Feichtinger 1860 BP).\*Bátaszék (Schneider 1909 W).\*Ercsi (Simonkovics 1875 BP).\*Érd (Perlaky 1891 BP).\*Sziget-újfalu (Tauscher 1872 BP; Z).\*Baja (Felföldy 1991 BP).\*Ráckeve (Degen 1918 BP).\*Tököl (Tauscher 1871 BP; PRC; W (2)).\*Kalocsa (Menyhárt 1876 BP).\*Szentendre (Vajda 1928 BP).\*between Dunaharaszt and Taksony (Degen 1915 BP; Boros 1919 BP).\*Insula Csepel (Kocsis 1909 BP).\*Soroksár (Sadler s. d. BP; Lengyel 1910 BRNM; Felföldy 1995 BP).\*Kunszentmiklós (Jávorka 1921 BP).\*Bugyi, Ürböpuszta (Boros 1925 BRNU; PR; W).\*Ócsa (Boros 1919 BP).\*Dabas (Kárpáti 1952 BP).\*Kecskemét, river Tisza [Tibiscum], meadow Sziksa (Dorner 1866 BP). \*Kecskemét (Boros 1920 BP).\*Lakitelek (Kováts 1927 BP; Szukó and Kováts 1979 BP).\*Szeged (Mayer 1855 W).\*Algjö (Kováts 1929 M).\*Kápolna (Sadler 1820 BP).\*Szarvas (Borbás 1884 BP).\*Rákos (Rosielkov 1908 BP; Jávorka 1917 BP).\*between Vésztő and Komádi (Borbás 1879 BP). **Czech Republic:** Libice nad Cidlinou (Tausch s. d. W).\*Svitavy (s. coll. s. d. BRNU).\*Drnholec (Bílý 1924 BRNM).\*between Dyjákovice [Dolní Dunajovice] and Mušov (Staněk 1921 BRNU).\*Mušov (Teuber 1899 BRNM; Bílý 1922 BRNM; Skřivánek 1923 BRNM (3)).\*between Pouzdřany and Mušov (Krist 1935 BRNU).\*Strachotín (? 1903 BRNM). **Slovakia:** Vysoká pri Morave (Novotný 1947 BRNM; Skřivánek 1949 BRNM).\*Zohor (Gayer 1916 BP).\*Láb, wet meadow (Nábělek 1935 SAV; 1936 BRA; Futák 1944 SLO (3)).\*Bratislava, insel Pečeň (Szép 1904 BRA).\*Bratislava, part Petržalka - Starý Háj [Alte Au] (Schneller s. d. SLO).\*Bratislava, river Dunaj, arm Rusovecké rameno [Karlburger Arm] (Scheffer 1922 Scheffer herb. in SLO).\*Svatý Júr, Nationale Nature Reservation (Holuby 1911 BRA; PR (2); PRC; 1912 PR; 1915 PR; PRC; 1921 BRA; Kavka 1937 BRA; PRC; Nábělek 1941 SAV (2); Futák 1942 SLO; 1947 SLO; Berta 1956 SLO).\*Čilstov (Májovský 1954 SLO).\*Dunajská Streda (Valenta 1937 BRNU).\*Baloň (Staněk 1946 BRNM).\*Klúčovec (Staněk 1948 BRNM).\*Vel'ký Meder (Weber 1935 PR).\*between Vel'ký Meder and Dolný Štál (Valenta 1937 BRA).\*Čalovo [Vel'ký Meder] (Májovský 1954 SLO).\*, Čalovo - Hanszeg (Májovský 1967 SLO (7)).\*between Čalovo [Vel'ký Meder] and Tôň (Májovský and Michalko 1951 SLO).\*Kolárovo (Hejný 1952 SLO (2)).\*Kolárovo, near the road to Komárno (Staněk 1936 BRNM).\*between Kameničná and Kolárovo (Valenta 1938 BRA; Krist 1938 BRNU).\*Martovce (Grulich 1988 MMI).\*Vrbová nad Váhom, settlement Zlatá Osada (Grulich 1989 MMI).\*Komárno (Futák 1949 SLO; Skřivánek 1961 BRNM).\*Komárno, settlement Kava (Grulich 1989 MMI).\*between Komárno and Hetín [Chotín] (Weber 1932 PR; Skřivánek and Weber 1936 BRA).\*mouth of rivers Dunaj and Hron (Kosinová 1975 PRC).\*Štúrovo (Ondráková 1952 PR).\*between Gabčíkovo and Komárno (Deyl 1959 PR (4)) – unmapped records. **Romania:** Periam (Wolfner 1858 W).\*Arad (Simonkai 1885 BP).\*Baziaș (Wierzbicki s. d. BP; Bohatsch 1878 BP).\*Lugoj (Heuffel 1820 W).\*Adea (Simonkai 1889 BP).\*Dubova (Simonkovics 1874 BP).\*Orșova (Jávorka 1912 BP).\*Dindești (Negrean 1965 M).\*Ciupercenii Noi, river Danube (Păun and Popescu 1968 BM; PRC; WU).\*Grădina (Richter 1894 Z).\*Somoava (Pallis 1913 BM).\*Maliuc (Kostková and Rydlo 1988 ROZ).\*Periprava (Rydlo 1987 ROZ).\*river Brațul Sfântu Gheorghe (Rydlo et al. 1985 ROZ). **Federal Republic of Yugoslavia:** Kusići, river Nera (Reuss 1868 W).\*between Perlez and Titel (Mayer 1968 M).

***Senecio paludosus* subsp. *lanatus* Holub**

**Hungary:** Tiszaroff (Perlaky s. d. BM; P; Z (2)).\*Szolnok - Abándszalók (Boros 1934 BP (2); Scheffer herb. in SLO; W).\*Rákos (Filarszky and Schilberszky s. d. BP; Lengyel 1900 PR; 1901 BP; PR; Dietz 1918 BP).\*Tiszaeszlár (Latzel 1894 BP).\*Tokaj, Bodrogköz (Hazslinszky s. d. W; 1854 Z; Hulják 1933 BP (2); 1935 BP) – unmapped records. **Czech Republic:** Libice nad Cidlinou (Sitenský s. d. PR). Dašice (Tausch s. d. PR; PRC). **Slovakia:** Oborín (Staněk 1947 BRNM). **Ukraine:** Buštyna (Vágner 1849 W; Z). **Romania:** Periam (Wolfner 1858 Z). **Byelorussia:** Weleśnica, distr. Pińsk, river Jasiołda (Twardowska 1895 BM; W) – unmapped records. **Russia:** Novočerkassk, near river Don (Jakušev 1910 BM).\*Sarepta, insel of river Volga (Becker 1853 BM; 1895 M).\*Sarepta (Becker 1871 Z).\*Chvalinsk, insel of river Volga (Gross 1925 BM).

***Senecio paludosus* subsp. *paludosus* <=> *S. paludosus* subsp. *angustifolius***

**Netherlands:** Voorst-Zutphen (Lindeman 1957 Z). **France:** Elbeuf (Debray 1913 Z).\*Creteil (Delacour 1858 P).\*Brienne-le-Château, river Aube (Retz 1972 M). **Germany:** Gundremmingen (Schuhwerk 1979 M).\*Palzing - Röhricht (Sellmair 1974 M).\*Pentling (Förther 1992 M).\*Geising (Schuhwerk 1984 M).\*Rhinow (Faalzow 1954 M).\*Reiten near Marquartstein (Vollmar 1936 M).\*Neuoffingen (Doppelbaur 1961 M). **Austria:** Baumgarten a. d. March (Juratzka 1857 BRA; Müllner 1878 W). **Czech Republic:** Radostín (Vitoušek 1885 BRNU (2)).\*Střeň (Otruba 1927 BRNU). \* Lanžhot, pri rieke Morava, 160 m a. s. l. (Staněk s. d. BRNM; Scheffer s. d. Scheffer herb. in SLO; Dvořák 1975 BRNU).\*Kostice (Staněk 1945 BRNM (2)).\*Rohatec (Rohrer 1820 PRC).\*Sudoměřice (Rohrer 1820 PRC).\*Moravský Písek (Bílý 1923 BRNU). **Slovakia:** Vysoká pri Morave, stream Rudávka (Dvořák 1949 BRNM). **Ukraine:** Buštyna (Vágner s. d. BP; W; 1865 BRA).